

Distribution patterns and population trends of breeding seabirds in the Aleutian Islands

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Running title: Distribution of breeding seabirds

ABSTRACT

The 1,800 km-long Aleutian archipelago is a breeding area for more than 10 million seabirds of 26 species. We evaluated the distribution of breeding colonies of 24 common breeding species in relationship to ocean passes of two sizes, availability of nesting habitat, and the distribution of introduced predatory mammals. Further we evaluated population trends and reproductive rates to amplify information about distribution. We compared distributions and demographic parameters based on proposed differences in marine habitats in the eastern, central, and western Aleutians. Samalga Pass did not appear to be a break point for breeding seabird distribution as is suggested for oceanographic characteristics and other species groups by papers in this volume. Factors affecting distribution varied with foraging and nesting strategies of various species groups. The three largest breeding aggregations of seabirds in the Aleutians (Buldir, Chagulak, and Kiska) all have relatively high species diversity and are located next to large passes. However, when other predictors were considered, proximity to medium or large passes was important mainly for surface-feeding piscivores. The extent of nesting habitat apparently does not limit the distribution of surface- or burrow-nesting species (including planktivores and piscivores). Instead, the distribution of these species probably has been shaped by introduced mammals. Nesting habitat for ledge- and crevice-nesting species is more limited than for surface- and burrow-nesters but is still fairly widespread. Ledge- and crevice-nesting species are less susceptible to fox predation than are surface- and burrow-nesters. These species may have been reduced by predation but were not extirpated.

Key words: Alaska, Aleutian Islands, invasive species, seabird distribution, seabird foraging patterns, seabird nesting habitat, seabird population trends

INTRODUCTION

The islands of the Aleutian Archipelago contain substantial breeding populations of 26 breeding species of seabirds totaling more than 10 million individuals (USFWS, 2000). The importance of the Aleutian Islands to marine birds was formally recognized in 1913 when the area was designated as one of the first National Wildlife Refuges. Currently, most of the islands are part of the Aleutian Islands Unit of the Alaska Maritime National Wildlife Refuge. This 1,800-km- long chain of islands which divides the North Pacific Ocean from the Bering Sea is the only land in this otherwise oceanic region, so various species of mobile seabirds have occupied nesting areas based on availability of nesting habitat in proximity to adequate prey resources. Introduced foxes had a devastating effect on the birds of most islands (Bailey, 1993), but partial restoration has occurred through active management (Ebbert and Byrd, 2002). The objective of this paper is to evaluate the relative importance of proximity to foraging habitat (particularly ocean passes at least 20 km wide), availability of nesting habitat, and presence of predatory mammals in shaping the current breeding distribution of the 24 most common species of seabirds in the Aleutian Islands. Distribution can be dynamic, so we present available data on population trends that foreshadow changes in distribution and on reproductive rates that suggest differences in prey availability or quality in different parts of the archipelago.

Availability of prey (forage fish and zooplankton) in relatively-close proximity to breeding sites influences the distribution of nesting seabirds (e.g., Hunt *et al.*, 1999, Springer *et al.*, 1999), because incubation shifts and particularly chick-rearing duties require foraging adults to return to the colony frequently (e.g., one or more times daily for most species

during chick rearing). Passes between islands may be particularly important foraging habitats for breeding seabirds because they are characterized by strong tidal currents, often overflowing sills, which bring nutrient-rich water to the surface and concentrate plankton, creating favorable feeding conditions for many species (e.g., Coyle *et al.*, 1992; Hunt *et al.*, 1998). Habitat characteristics (e.g., volume of flow, salinity, temperature) of passes vary throughout the Aleutians. For instance, passes in the eastern Aleutians (Unimak Pass to Samalga Pass) differ from passes in the central Aleutians (west of Samalga Pass as far as Amchitka Pass) in that the eastern passes are relatively shallow and the primary water flowing north through the eastern passes is from the Alaska Coastal Current which is relatively fresh and warm (Ladd *et al.* 2005). Also, nutrient transport is lower in the eastern passes than in central Aleutian passes (Mordy *et al.* 2005). Additional transition zones, like the one identified at Samalga Pass, may occur further west (Logerwell *et al.* 2005).

In addition to foraging considerations, the availability of suitable nest sites affects seabird distribution. Except for the extreme eastern and western ends, the treeless Aleutians are devoid even of shrubs. As a result, nesting habitat for seabirds is either on or beneath the surface of the ground.

Because of extirpations or serious reductions in bird populations resulting from predation or habitat destruction from introduced mammals (Bailey, 1993), nesting and foraging habitat availability alone may not explain the current distribution and relative abundance of seabirds in the Aleutian Islands. Typically, most species of marine birds nest on remote islands because they are free from terrestrial predators. This was true historically throughout the Aleutian Islands, west of Umnak Island (Murie, 1959). Soon after Bering's voyage in 1741, foxes were introduced to some of the Aleutians for fur production, and the

practice continued until 1930, when most islands had been “stocked” (Bailey, 1993). Purposeful introductions of reindeer and other ungulates, ground squirrels, and several small mammals also occurred, and rats were accidentally introduced to a number of islands in cargo or during shipwrecks (Ebbert and Byrd, 2002). After World War II, the Refuge began a fox removal program. Since that time 38 islands (comprising more than 4 thousand km²) have been cleared of foxes. Although foxes had extirpated a number of bird species from large islands, remnant breeding populations often persisted on offshore islets and many of these species quickly expanded to nearby larger islands once foxes were removed (e.g., Byrd *et al.*, 1994). As a result of the restoration program, the current distribution and relative abundance of seabirds includes recovered, recovering, and still depressed (on islands where foxes remain or were only recently removed) populations.

In this paper, we evaluate the influence of the three main factors listed above (passes, nesting habitat, and predatory mammals) on the distribution, population trends and productivity of nesting seabirds. Further, we evaluate the relative abundance and species composition of breeding seabirds at colonies in different parts of the archipelago in relationship to differences in marine habitat suggested by Ladd *et al.* (2005), Logerwell *et al.* (2005) and Jahncke *et al.* (2005).

METHODS

For organizational purposes and to facilitate understanding the causes of seabird distribution, we classify seabirds as either piscivores (primarily feeding on fish) or planktivores (primarily feeding on plankton), and within these categories, we noted that species employ various foraging strategies (e.g., diving vs. surface-feeding and nearshore vs. offshore feeding) (Table 1). Further, based on their breeding strategies, seabirds are classified as crevice-nesters (eggs are laid inside crevices within talus fields, boulder-strewn beaches, and cracks in cliffs); burrow-nesters (these species excavate tunnels to nest sites in soil); ledge-nesters (eggs are laid on ledges on cliff faces); or surface-nesters (eggs are laid on the ground).

Data collection

Information about seabird distribution came from the Beringian Seabird Colony Catalog (USFWS, 2000) and recent surveys not yet in the database conducted by Alaska Maritime NWR staff (Appendix A). Most of the data for the Aleutian Islands came from systematic surveys of every island in the late 1970s and early 1980s (e.g., Day *et al.*, 1978, Day *et al.*, 1979) and more recent surveys of many of the main colonies by refuge personnel in the 1990s (e.g., Byrd and Williams, 1996; Byrd *et al.*, 2001). In the Beringian Seabird Colony database (USFWS, 2000), more than one breeding colony per island is often recorded, nevertheless, we combined all the colonies on an island for assessing distribution. We had data for 128 islands in the Aleutians where one or more species of seabird nests. The counts vary in quality based on survey effort (i.e., varies from replicated rigorous censuses at islands that are visited often, to a single count for islands visited infrequently) and difficulty of

counting (e.g., crevice nesters and extremely large colonies are very difficult to survey). Nevertheless, because colony sizes vary over six to seven orders of magnitude and enter the model in a log scale, survey errors are unlikely to have an impact on the statistical models. Trend data come from an annual seabird-monitoring program initiated by the Alaska Maritime NWR in the mid-1970s, primarily at three sites (Buldir in the western, Kasatochi in the central, and Aiktak in the eastern Aleutians). The central Aleutians monitoring site actually consists of three islands that are visited annually (Kasatochi, Koniuji and Ulak) to provide data about the full suite of breeding species in that region. In some cases, we have additional trend data from other islands in the Aleutians that are visited less regularly.

Population trend data for each species were derived from time series of counts on index plots, usually not censuses of the entire colony. We include data for species with peer reviewed monitoring techniques. Standard census and monitoring methods are well developed for ledge-nesting and surface-nesting seabirds (e.g., Walsh *et al.*, 1995). Because they are visible to observers at nest sites, these species lend themselves to precise counting practices, although the highly variable attendance of some species (e.g., northern fulmars, *Fulmarus glacialis*) at colonies can cause confidence intervals to be large. For ledge nesters, we used counts of adult birds visible on a plot; counts of plots were replicated 5 or more times during each nesting season. For burrow-nesters, we used counts of burrow entrances (i.e., potential nest sites) as an index to population size. Trends of crevice-nesting seabirds are based on indices of abundance during peak attendance of birds on the surface of colonies (auklets, *Aethia* spp.) or at sea counts near breeding colonies (pigeon guillemots, *Cephus columba*). Monitoring methods are poorly developed for most species of crevice-nesters and therefore we omit trend estimates for these species.

Productivity data were collected at long-term monitoring sites for many species (see Dragoo *et al.*, 2001). Productivity monitoring consisted of tracking a sample of nests through time to determine reproductive success (chicks fledged per nest).

Data analysis

To model seabird distribution we fitted a linear model with four predictor terms without interactions for each of the 19 species/species pairs. We used the natural log of the total number of birds ($\ln(n+1)$) of a species per island as the dependent variable. Log-transformation was necessary to normalize the count data and to reduce the influence of the few very large colonies. The four predictor variables were: distance to nearest medium-sized pass (> 20 km wide gaps cutting across the main axis of the chain which are less than 500 m deep), distance to the nearest large pass (also > 20 km wide but deeper than 500 m, i.e. Buldir, Amchitka and Amukta passes, Fig 1), natural log of the island area, and geographical island group within the Aleutians (western: Near Islands to Amchitka Pass; central: between Amchitka and Samalga Pass; or eastern: between Unimak and Samalga Pass – Fig. 1). Differences in predicted colony size based on different factors indicates variability in distribution (i.e., if a particular species was evenly distributed, the predicted colony size would be the same for every factor). To determine distance of an island from a pass we measured on a map from the center of the island to the closest edge of the pass to the nearest km. We chose the center of the island since we combined counts from all colonies of a species on each island. We were unable to include a quantitative analysis of affects of mammalian predators in the model because of the various degrees of restoration that are occurring currently. For example, introduced foxes have been removed from about 40 islands

since 1970, but recovery periods for these islands range from 1-35 years, and species recover at different rates. As a result, the influence of mammalian predators on current distribution of breeding seabirds was evaluated more qualitatively. To evaluate the significance of model terms we used “single term deletion” (Venables and Ripley, 2002), comparing the full model with a reduced model that does not contain the term in question. When the factor “island group”, i.e., geographic area was significant, indicating that the abundance of a species varied among island groups, multiple comparisons (R package “multcomp”, Westfall, 1997) were conducted comparing each island group (e.g., Eastern) with the average of the others. P-values were Bonferroni adjusted. To clarify distribution patterns, we used the linear model to predict mean colony size in each island group with the other factors held constant. A significance level of $p=0.1$ was used throughout. All statistical analyses were conducted in the software environment R v1.9.0 (R Development Core Team, 2003).

RESULTS

In the following accounts we evaluate the distribution and relative abundance of each species of breeding seabird based on available information about foraging and nesting strategies and the distribution of introduced mammals. When available, we present population trend and productivity indices for species at selected long-term monitoring sites in the western, central, and eastern Aleutians (see Dragoo *et al.*, 2001). The species accounts are structured first by feeding guild (planktivore or piscivore), and, within those groupings, are ordered by nesting strategy.

Planktivores

Crevise nesters.

Least and crested auklets (*Aethia pusilla* and *A. cristatella*) occur in 8 mixed-species colonies clustered in the western and central Aleutians (Fig. 2). They are not found in the extreme western Aleutians (Near Islands) or in the eastern Aleutians. Nearly half of the Aleutian breeding population of least auklets occurs at Kiska Island (several million birds), and nearly 90% of both species breed between Buldir and Gareloi islands (Gareloi is located immediately east of Amchitka Pass). There was weak evidence (p values slightly greater than 0.1) that breeding colonies occur in proximity to medium passes (Table 2). The model confirmed that the largest nesting colonies are clustered within the western Aleutians (Table 3). Nesting habitat is patchy in the Aleutians, and it tends to degrade as weathering fills crevices with debris, and vegetation encroaches. New rock falls or volcanic eruptions periodically create new habitat (e.g., Gaston and Jones, 1998), so at least locally, distribution

is dynamic on a decadal to century scale. Nevertheless, there appears to be available crevice habitat (particularly cliff crevices and boulder strewn beaches like those used by auklets on islands farther north in the Bering Sea--e.g., in the Pribilof Islands) in the Aleutians both east and west of the current distribution of these species. Introduced foxes prey on these auklets (Murie, 1959) and may reduce populations, but most nest sites are safe from foxes so extirpation is uncommon. Rats can potentially extirpate auklet colonies, but it is unknown whether this has happened in the Aleutians.

As indicated in methods, we do not have precise methods of monitoring population trends in crested and least auklets. The only site where we have an annual “surface count” survey is Kasatochi and that index does not indicate significant population trends (Dragoo *et al.*, 2001). The environments in the western and central Aleutians apparently were similar for auklets because average productivity rates for the two areas (western—Buldir, central—Kasatochi) were nearly identical (Fig. 4).

Whiskered auklets (*Aethia pygmaea*) occur in many small colonies throughout the entire Aleutians (Byrd and Williams, 1993; Williams *et al.*, 2003). In fact they have been recorded on nearly 40% of all the islands with seabird colonies of any type (Table 4). Notable concentrations occur at Buldir, in the islands between Adak and Great Sitkin, Seguam, the Islands of Four Mountains, and the Baby Islands (Fig. 2), but we found no significant differences in occurrence among island groups (Table 3). Nevertheless, larger islands tended to have larger colonies (Table 2). Interestingly, except for Buldir, major concentration areas for whiskered auklets are largely devoid of least and crested auklets. According to the model, proximity to neither large nor medium passes was an important factor for determining whiskered auklet distribution (Table 2). These auklets forage mostly

in tide rips (Byrd and Williams, 1993) near passes smaller than the scale we used in our analysis. Whiskered auklets are apparently highly susceptible to predation by introduced foxes and rats, partially because juveniles return to land after fledging (unlike other *Aethia* auklets) (Zubakin and Konyukhov, 2001). Following fox-removal, the species probably will re-occupy most of its former range except for islands with rats. In fact, there is evidence of recent population increase and probably expansion (Williams *et al.*, 2003). We have no time series population data for whiskered auklets, and productivity is measured only at Buldir, so comparisons across locations are not possible.

Parakeet auklets (*Aethia psittacula*) have a similar distribution to that of whiskered auklets, in that they occur mostly in relatively small groups at a number of locations throughout most of the Aleutians (Fig. 2), and they nest in similar habitats. One difference in the distribution of the two species is that very few parakeet auklets are found in the Eastern Aleutians, whereas a major concentration of whiskered auklets occurs near the Baby Islands. Parakeet auklet populations differ in abundance among island groups (Table 2). There are two large breeding concentrations (Gareloi and Buldir which together contain 84% of the total estimated Aleutian population). Indeed, the western Aleutians have the highest mean colony count (Table 3). Like whiskered auklets, parakeet auklets were more common on larger islands (Table 2), a factor likely explained by the tendency of both species to use boulder-strewn coastlines and rock crevices on coastal cliffs. Most of the 35 parakeet auklet colonies in the Aleutians contain fewer than 200 birds. The paucity of parakeet auklets in the eastern Aleutians (Table 3) is noteworthy because the species has large colonies east of the Aleutians in the Shumagin and Semidi Island groups. We found no relationship between nesting locations and passes (Table 2). As described for crested and least auklets, introduced

mammals have probably reduced populations but not limited distribution. In fact, the largest breeding colony of parakeet auklets, on Gareloi Island, had foxes until 1996 (Paragi, 1996). We have no time series population data for parakeet auklets, and productivity is measured only at Buldir, so comparisons across locations are not possible.

Burrow nesters.

All species of burrow-nesters in the Aleutians show apparently similar distributions (Fig. 2). Four planktivorous species (Leach's and fork-tailed storm-petrel, *Oceanodroma leucorhoa* and *furcata*, ancient murrelet, *Synthliboramphus antiquus*, Cassin's auklet, *Ptychoramphus aleutica*) occur in a patchy distribution throughout the Aleutians, with the largest colonies on Buldir, Koniugi and Chagulak. Smaller colonies occur in relatively dense concentrations in the eastern Aleutians.

Leach's and fork-tailed storm- petrels, which usually nest in mixed-species colonies, are the most abundant burrow-nesting planktivores in the Aleutians and occur on 51 islands (Table 4). The 3 largest colonies range from 25,000 to 3 million birds. Many of the other colonies contain thousands of birds (Appendix A). Model results suggest that storm-petrel breeding areas had no affinity to passes (Table 2). For nesting, they typically dig earthen burrows in densely-vegetated slopes, but also nest in rock crevices or under debris. These habitats are very common and widespread in the Aleutians. Storm-petrels probably were easily extirpated from a number of islands by introduced foxes and rats (Murie, 1959; Bailey, 1993). Recovery is now underway following fox removal (e.g., at Kasatochi, J.C. Williams, unpubl. data), but no recovery is possible on islands with rats. The prey base for these plankton feeders apparently has been good near annual monitoring sites in the eastern

(Aikta) and central (Ulak in the Kasatochi area) Aleutians, where introduced mammals are not a factor, because storm-petrel populations have increased recently (Fig. 3). In the western Aleutians (Buldir), there is no evidence of substantial change in population size since data collection began in the mid-1970s (Fig. 3). Productivity indices for fork-tailed storm-petrel at Buldir (w. Aleutians), Ulak (c. Aleutians), and Aikta (e. Aleutians) indicate similar conditions in all areas (Fig. 4).

Ancient murrelets and Cassin's auklets occur in relatively small colonies (largest 3 colonies are 3,000 to 10,000; but most are less than 500 – Fig. 2) scattered throughout the Aleutians. The two species occur in similar habitats, often in mixed-species colonies with storm-petrels. Ancient murrelets were found in 40 locations, whereas Cassin's auklets are known from only 20 sites (Table 4). The distribution of these species did not vary among groups (Table 3). Both species seemed to have negative relationships with passes, Ancient murrelets with large passes and Cassin's auklets with medium passes (Table 2). Both species dig earthen burrows in sloping vegetated hillsides, a habitat type that is very common and widespread in the Aleutians. The distribution of large colonies of these species shows strong concordance with historical absence of mammals (e.g., the largest multi-species colonies at Buldir, Koniugi and Chagulak never had foxes or rats). Historically, ancient murrelets and Cassin's auklets almost certainly occurred on more islands than they do currently. The patchy current distribution is most likely a result of extirpations by introduced foxes and rats, and differential rates of recovery following fox removal. These species are active on land only at night, and likely remain undetected at some locations. We have no data on population trends or productivity.

Piscivores

Ledge nesters.

Pelagic and red-faced cormorants (*Phalacrocorax pelagicus* and *P. urile*) nest on 63% of seabird islands throughout the Aleutians typically in fairly small colonies (<200 birds, Fig. 2, Appendix A). Based on best estimates from the colony database, more than half the breeding populations for these species occur in the Near Islands (the westernmost group in the western Aleutians). Consequently, the western Aleutians as a group have significantly higher predicted average colony sizes than the central Aleutians or eastern Aleutians, and the eastern Aleutians had larger averages than the central Aleutians (Table 3). Cormorants nest and roost on broad ledges (e.g., Squibb and Hunt, 1983) and on tops of rocky islets (e.g., Hobson, 1997). These habitats are widespread and fairly common throughout the Aleutians. The model indicated that cormorant numbers are related to island size (Table 2), which we expect to be proportional to coastline length.

The distribution of cormorant colonies is not related to distance from passes (Table 2). Both species of cormorants are nearshore divers, usually foraging within 3 km of land (e.g., Wehle, 1976), although red-faced cormorants apparently can feed in deeper water than pelagic cormorants and they occasionally have been seen up to 20 km offshore (Causey, 2002). There appears to be a strong relationship between the amount of feeding habitat (i.e., shallow water near breeding areas) and cormorant densities: the Near Islands contain both the most cormorants and the most extensive shallow water area of any of the island groups. Judging from the areas used by cormorants for nesting following fox removal, it is clear that on some islands, introduced mammals limited the distribution of cormorants (G.V. Byrd,

unpubl. data), but currently the overall distribution of cormorants probably is not limited by mammalian predators or by nesting habitat. The distribution of cormorants was positively related to island size indicating wide distribution on large islands (Table 2), including some that still have foxes.

Although cormorant numbers at monitoring sites are highly variable among years, there is evidence that they have declined at the eastern Aleutian monitoring site (Aikta) and there is other regional evidence of decline (e.g., at Amak, Byrd *et al.*, 2001). No overall trends are evident at the central (Kasatochi) or western (Buldir) monitoring sites (Fig. 3), but recent surveys throughout the Near Islands suggest substantial declines have occurred there since the 1970s (Byrd and Williams, 2004). Productivity indices for pelagic cormorants in the western Aleutians (Buldir) and central Aleutians (Kasatochi/Koniuji) appear to be similar (Fig. 4).

Double-crested cormorants (*Phalacrocorax auritus*) occur in small colonies (<200) in the eastern Aleutians as far west as the Islands of Four Mountains where the species reaches its northwestern distribution limit (Hatch and Weseloh, 1999). We did not differentiate double-crested cormorants from the other species in the model because cormorants were not always identified to species during surveys. We have no population trend or productivity data on this species.

Black-legged kittiwakes (*Rissa tridactyla*) are a circumpolar species with 15 colonies in the Aleutians scattered throughout the chain (Fig. 2, Table 4). The largest, at Buldir Island, contains 45,000 birds; other relatively large colonies are at Agattu, Koniuji, Chagulak and Bogoslof – all less than 8,000 birds. The average colony was larger in the western Aleutians than farther east (Table 3). Black-legged kittiwakes have significant affinities for

nesting near large passes but the species had a negative relationship with medium passes (Table 2). In contrast to the widespread distribution of black-legged kittiwakes, red-legged kittiwakes (*Rissa brevirostris*) are endemic to the Bering Sea (Byrd and Williams, 1993). About 20% of the world's population of red-legged kittiwakes occurs in the Aleutians, primarily at Bogoslof (eastern Aleutians) and Buldir islands (western Aleutians). The remainder occur in the Pribilof and Commander islands. Three new, small red-legged kittiwake colonies have become established recently (at Koniuji and Unalga, central Aleutians, and Amak, eastern Aleutians (J.C. Williams and G.V. Byrd, unpubl. data) indicating an expansion of range. Although we saw no effect of passes on distribution, too few colonies are present to allow rigorous evaluation., but apparently nesting habitat is not limiting distribution based on the recent expansions. Both species of kittiwakes have increased since the mid-1970s at Buldir (Fig. 3), a trend confirmed at nearby Agattu for black-legged kittiwakes (Williams and Byrd, 1992), and at Bogoslof for both species (Byrd, 2002). In the central Aleutians, black-legged kittiwakes were fairly stable between 1980 and 2000 (Dragoo *et al.*, 2001).

Productivity data for both species is highly variable between years and across sites. Buldir in the western Aleutians appears to have generally lower productivity than Bogoslof in the eastern Aleutians (Fig. 4).

Thick-billed (*Uria lomvia*) and common murres (*U. aalge*) occur in mixed-species colonies on 37 islands in the Aleutians (Fig. 2, Table 4). Thick-billed murres are much more numerous but a few common murres are present in most colonies and a few colonies are composed entirely of common murres. Murre distribution did not vary among island groups (Table 3). The largest colonies (each with 10,000 – 40,000) are scattered throughout the

chain (e.g., Buldir, Chagulak, Kagamil, and Bogoslof islands). There was no evidence of affinities for passes, nor did island size appear to have an effect on the distribution of colonies (Table 2). Cliff nesting habitat is widely distributed in the Aleutians, and it is not apparent that lack of this type of habitat limits murre distribution. Ledge-nesting murre were probably not extirpated anywhere by introduced foxes, but common murre may have been excluded from cliff-top nesting areas they sometimes use in the absence of mammalian predators. In the western Aleutians, murre have increased at Buldir (Dragoo *et al.*, 2001) and Agattu (Williams and Byrd, 1992) between the mid-1970s and 2000. Interestingly, a local shift in nesting locations appears to be occurring in the central Aleutians where population increases at Koniugi coincide with a decline at nearby Kasatochi (Dragoo *et al.*, 2001, Barton and Lindquist, 2003). Numbers have been highly variable, but without apparent trend since 1990 at Aiktak in the eastern Aleutians.

Thick-billed murre on Buldir, Kasatochi, and Aiktak appear to exhibit higher average productivity in the western Aleutians than farther east (Fig. 4). Common murre productivity has been similar in the eastern and western Aleutians, but the small colony at Kasatochi had slightly lower rates than elsewhere largely due to an unusually large number of failure years.

Crevise nesters.

Horned puffins (*Fratercula corniculata*) occur on over 60% of the seabird nesting islands in the Aleutians (Fig. 2, Table 4). Relatively large colonies occur in the western Aleutians compared to farther east (Table 3). The distribution of nesting colonies was related to island size, an intuitive conclusion because the species nests in cliff crevices, thus the relationship

to amount of coastline. Like crevice-nesting auklets, horned puffins are notoriously difficult to count, so estimates are imprecise. The largest concentration east of Samalga Pass is Unalaska where only a few hundred birds occur, whereas there are 14 colonies in the western and central Aleutians with over 1000 birds each. The largest colony in the Aleutians is about 20,000 birds at Buldir. These habitats are fairly common and widespread in the Aleutians. Introduced foxes probably did not extirpate horned puffins. We have no population trend or comparative data on productivity for this species.

Burrow nesters.

Tufted puffins (*Fratercula cirrhata*) are found on more than 80% of the seabird nesting islands in the Aleutians (Fig. 2, Table 4), in colonies ranging from 200 to 163,000 (Egg Island, eastern Aleutians). Predicted values from the model show the species most abundant in the western Aleutians, and fewer than expected, if the species was evenly distributed, occur in the eastern Aleutians, in spite of a few large colonies there (Table 3). Tufted puffin nesting colonies were significantly distant from large and medium passes compared to the mean prediction (Table 2). Fox introductions had a major impact on tufted puffin populations (e.g., Bailey, 1993; Byrd *et al.*, 1994), but because the species could persist in small numbers on offshore islets, recolonization following fox removal has been comparatively rapid on islands without rats. Tufted puffin populations have increased at all monitoring sites since the mid 1980s when monitoring began (Fig. 3). Productivity indices at Buldir and Aikta appear quite similar (Fig. 4).

Surface nesters.

Northern fulmars nest on only 8 islands in the Aleutians (Attu, Buldir, Davidof, Ulak, Gareloi, Amukta, Bobrof and Chagulak), with 97% of the entire breeding population found at Chagulak (Fig. 2). Large, but not medium, passes play an important role in distribution (Table 2), and the largest colonies (Chagulak, Amukta, Gareloi, Buldir) are all near passes. In the Aleutians, fulmars are surface-nesters, digging nest scrapes on steep grassy sea-facing hillsides on islands where mammals have never been introduced. This habitat is widespread in the Aleutians, but it would have been accessible to introduced foxes. Elsewhere in Alaska (e.g., the Pribilof Islands), at colonies where foxes or ground squirrels are native, fulmars nest on ledges. Given their ability to nest on cliffs where foxes are native, it appears that something other than predation limits them to relatively few colonies. In areas of high food concentration (e.g., Ingestrom rocks area in the western Aleutians), often many more birds are observed feeding than are known to nest within hundreds of miles. We do not know whether most of these are non-breeders or whether the birds have traveled extremely far to feed. Fulmars have recently reoccupied Attu following fox removal (Byrd and Williams, 2004), and populations at Buldir appear to be increasing and expanding on the island (J.C. Williams, unpubl. data). We have no population trend or productivity data for this species at the large Chagulak colony.

Glaucous-winged gulls (*Larus glaucescens*) occur on 83% of the seabird islands in the Aleutians (Table 4), with lower numbers per colony in the central Aleutians than west of Amchitka Pass or east of Samalga Pass (Table 3, Fig. 2). The largest colonies are Attu (5818) and Buldir (5000), but there are 16 colonies with >1000 birds. Gulls tended to be

more common on large islands (Table 2). Glaucous-winged gull distribution was not related to large or medium passes (Table 2).

These ground-nesting gulls have abundant nesting habitat, but their breeding distribution was reduced by introduced foxes (Murie, 1959). Nevertheless, at some sites gulls have recovered quickly since fox removal (Byrd *et al.*, 1994). Prey rather than available nesting habitat is probably the current limiting factor to their population size. Glaucous-winged gull populations have decreased at all long-term monitoring sites in the Aleutians since the mid 1970s (Fig. 3), although in several cases an increase was documented immediately following fox eradication (Byrd *et al.*, 1994). Productivity rates have been lower at Buldir in the western Aleutians than at Aiktak in the eastern Aleutian (Fig. 4).

Marbled (*Brachyramphus marmoratus*) and Kittlitz's murrelets (*B. brevirostris*) are thought to breed on up to 6 islands in the Aleutians (Attu, Agattu, Adak, Atka, Unalaska, and Unimak) (Day *et al.*, 1999 and G.V. Byrd, unpubl. data) (Fig. 2), most of which are over 1,000 m at their highest points, and offer persistent snow fields. Each also has protected bays in the vicinity. The two species seem to occur together everywhere, although species have not been identified separately on many surveys. *Brachyramphus* murrelet distribution had a strong relationship to island size, and colonies tended to be located relatively far from passes (Table 2). Nesting in the Aleutians apparently occurs on high elevation scree slopes. Although marbled murrelets nest in trees elsewhere in their range (Nelson, 1997), they are ground nesters, probably at high elevations in the Aleutians. Murrelets persisted on each of the breeding islands in the presence of introduced foxes. We have no population trend or productivity data for these species.

Aleutian and Arctic terns (*Sterna aleutica* and *S. paradisaea*) breed very locally throughout the Aleutians. These terns breed in mixed-species colonies at 7 colonies (Fig. 2). The largest concentration is at Amchitka Island, in the Rat Islands. Both species tended to occur on larger islands relatively near large passes (Table 2). Both species of terns have an affinity for nesting near large passes (Table 2). These species were probably affected by fox predation, but apparently are able to sustain populations where rats are present (e.g., Amchitka and Adak). We have no population trend or productivity data for these species.

DISCUSSION

It is self-evident that, to successfully breed, seabirds need regular access to adequate prey resources and appropriate nesting habitat that is safe from predators. In the Aleutians, it is not always obvious which factor or combination of factors drives the current breeding distribution of various species. In the results section we evaluated factors affecting the distribution of each species, but here we discuss commonalities among species in the way they are affected by various factors. In spite of differences in oceanographic conditions described for passes east and west of Samalga Pass (e.g., Jahncke *et al.*, 2005; Ladd *et al.*, 2005), this location did not appear to be a break point for breeding seabirds. Nevertheless, we did note differences in species assemblages that could indicate fundamental differences in foraging habitat.

The distribution and abundance of seabird prey (various types of nekton and plankton) is related to characteristics of marine habitat (e.g., Kinder *et al.*, 1983, Springer *et al.*, 1996, Springer *et al.*, 1999). For example, the Near Island group in the western Aleutians, which has a relatively extensive shelf area, contains relatively large concentrations of species (e.g., cormorants, common murre) that feed over shallow water on forage fish like sand lance (*Ammodytes hexapterus*) and relatively low numbers of species (e.g., crested and least auklets) that feed on pelagic prey, e.g., oceanic copepods like *Neocalanus* spp. (see Springer *et al.*, 1996).

Our general linear model (Table 2) suggests that proximity to large, but not medium-sized passes, was important for surface-feeding piscivores (e.g., northern fulmars, terns, and kittiwakes). Conditions, particularly at the edges of these wide, deep passes must routinely concentrate forage fish prey.

Since the largest crested and least auklet colonies were located near moderate passes, we suspect passes are also important to these species for foraging. The model did not detect this effect (p values larger than 0.1), probably because of low statistical power associated with small numbers of colonies and widely varying colony sizes. Although the model did not find a significant relationship between the distribution of whiskered auklets and major passes, the species is known to concentrate in “tide rips” or small passes where convergent fronts form (Byrd and Gibson, 1980). Because passes are known to concentrate plankton and bring it to the surface (Hunt *et al.*, 1998), we would expect *Aethia* to benefit from feeding in these situations. Parakeet auklets were the only species of *Aethia* that clearly had no affinity for passes. This may be explained by their foraging behavior, i.e., feeding singly or in small flocks on thinly distributed prey in a variety of habitat (Hunt *et al.*, 1998; Jones *et al.*, 2001).

There was no evidence that either murrelets or most nearshore feeders (cormorants, gulls, terns, *Brachyramphus* murrelets, and guillemots) nested near passes. The nearshore species typically forage in shallow water where upwelling, currents, and fronts are not as likely to affect the distribution of prey as for more pelagic foragers.

We found a positive relationship between island size (area) and breeding colony size for most of the nearshore feeding species (cormorants, gulls, terns, *Brachyramphus* murrelets, pigeon guillemots, parakeet auklets, whiskered auklets, and horned puffins). Interestingly this group of species includes birds that use different types of nesting habitat (i.e. ledges, crevices, and the surface). Clearly, appropriate nesting and foraging habitats for *Brachyramphus* murrelets are only available on larger islands, but it is not so clear why the relationship exists for the other species. Nevertheless, a common characteristic is that these

species are able to find nesting habitat in proportion to its availability (Table 4). Availability of foraging habitat probably also influences this relationship. Large islands may have more shelf (shallow water) feeding habitat nearby than smaller islands.

The lack of a relationship between island size and the distribution of other species suggests nesting habitat is patchier and not related to island size. For some of these other species, distribution is probably affected by factors other than nesting habitat.

Probably burrow and surface nesters (except terns and *Brachyramphus* murrelets) are not habitat limited anywhere in the Aleutians, and their distribution (across many different feeding guilds) appears to reflect distribution of predatory mammals. Not all available cliff habitat seems to be occupied by ledge-nesters and it is not clear why some islands are selected and not others.

The degree of colonialism varied among the breeding species that we evaluated in the Aleutians. For example, of all species, pigeon guillemot was present on the largest number of islands (85%) but in the lowest total abundance (Table 4). Conversely, least auklet was present only on 6% of the islands but was the second-most abundant seabird.

Foxes, native in the Fox Islands, and introduced elsewhere, have played a major role in shaping the geographic distribution of ground- and burrow- nesting seabirds (Bailey, 1993). Populations of most crevice-nesting and ledge- nesting species were probably reduced but not extirpated by foxes (but see Williams *et al.*, 2003 for whiskered auklets). The effect of predatory mammals is evident from the near-perfect concordance of large colonies of surface and burrow nesters with islands that were historically free of terrestrial mammals (e.g., Buldir, Koniuji, Chagulak). In some cases like whiskered auklet, the species could have already recovered substantially after fox eradication (Williams *et al.*, 2003). There is

ample evidence that foxes have a disastrous effect on storm petrel populations (e.g., Bailey, 1993). The distribution of least and crested auklets probably has not been changed due to introduced mammals, nevertheless, foxes, ground squirrels, and particularly rats probably have reduced populations. Small offshore islets have played a role in conserving populations of surface and burrow-nesting species by acting as refuges where small populations could nest when main islands were infested with introduced mammals. Once mammals are removed, these small populations act as founder stocks to reestablish main island populations (E.P. Bailey, unpubl. data).

For the 9 cases where we could compare average rates of productivity among geographic portions of the Aleutians, only a few differences were evident (Fig. 4). Gulls and kittiwakes seemed to have lower productivity in the western Aleutians than in the central (kittiwakes only) and eastern Aleutians, and murrelets tended to have slightly lower success rates in the central Aleutians than elsewhere. Overall, though there were no fundamental patterns that would suggest substantial differences in the “quality” of the regions from the viewpoint of breeding marine birds.

Combinations of the factors discussed above or additional factors may be influencing the current distribution of seabirds in the Aleutians. No single factor seems to explain the high concentrations of seabirds in a few colonies; 64% of the breeding birds in the Aleutians occur in 3 colonies and 89% occur in 12 locations. There was a significant positive correlation ($r = 0.73$, $p < 0.001$) between large numbers of birds and high species diversity. Most of these large, diverse colonies are near major passes, but not all. Only about half never had foxes.

We found little evidence of competitive exclusion among most species. Nevertheless, the relatively low populations of whiskered auklets at most large colonies of least and crested auklets, suggests competition may be a factor. However, whiskered auklets are not always excluded by these more common species, as evidenced at Buldir and Koniuji where large concentrations of all three species occur.

Philopatry, social interactions, and predator avoidance may limit some species, e.g., ledge-nesting piscivores like fulmars, murres, and kittiwakes. These species apparently have much more nesting habitat and food available than they use. Empty ledges are widespread throughout the Aleutians, and other piscivores with similar prey (e.g., tufted puffin) are more widespread than these species.

Trend data from monitoring sites indicates that no species show a widespread decline across the Aleutian Islands except three nearshore species – cormorants, glaucous-winged gulls and pigeon guillemots. Timing of the decline appears remarkably coincident with a documented region-wide decline in sea otters (which use the same foraging zone) and a related change in the kelp forest whereby sea urchins have increased dramatically and kelp is substantially diminished (Estes *et al.*, 1998).

ACKNOWLEDGEMENTS

We thank Shawn Stephensen for providing Beringian Seabird Colony Catalog data and maps, and Don Dragoo for providing population trend graphs. Joel Reynolds helped with statistical analyses. Jeff Williams supervised most of the field crews in the Aleutians, providing training, guidance, logistics, and technical assistance. The crew of the M/V Tiglax (captain: Kevin Bell) has provided essential logistical support in the Aleutians throughout almost the entire study period. George Hunt, Gordon Kruse, Peter Dunlevy, and two anonymous reviewers provided helpful comments on the manuscript. Finally, we thank the many field crews who collected data at each of the monitoring sites, whose names are too numerous to mention.

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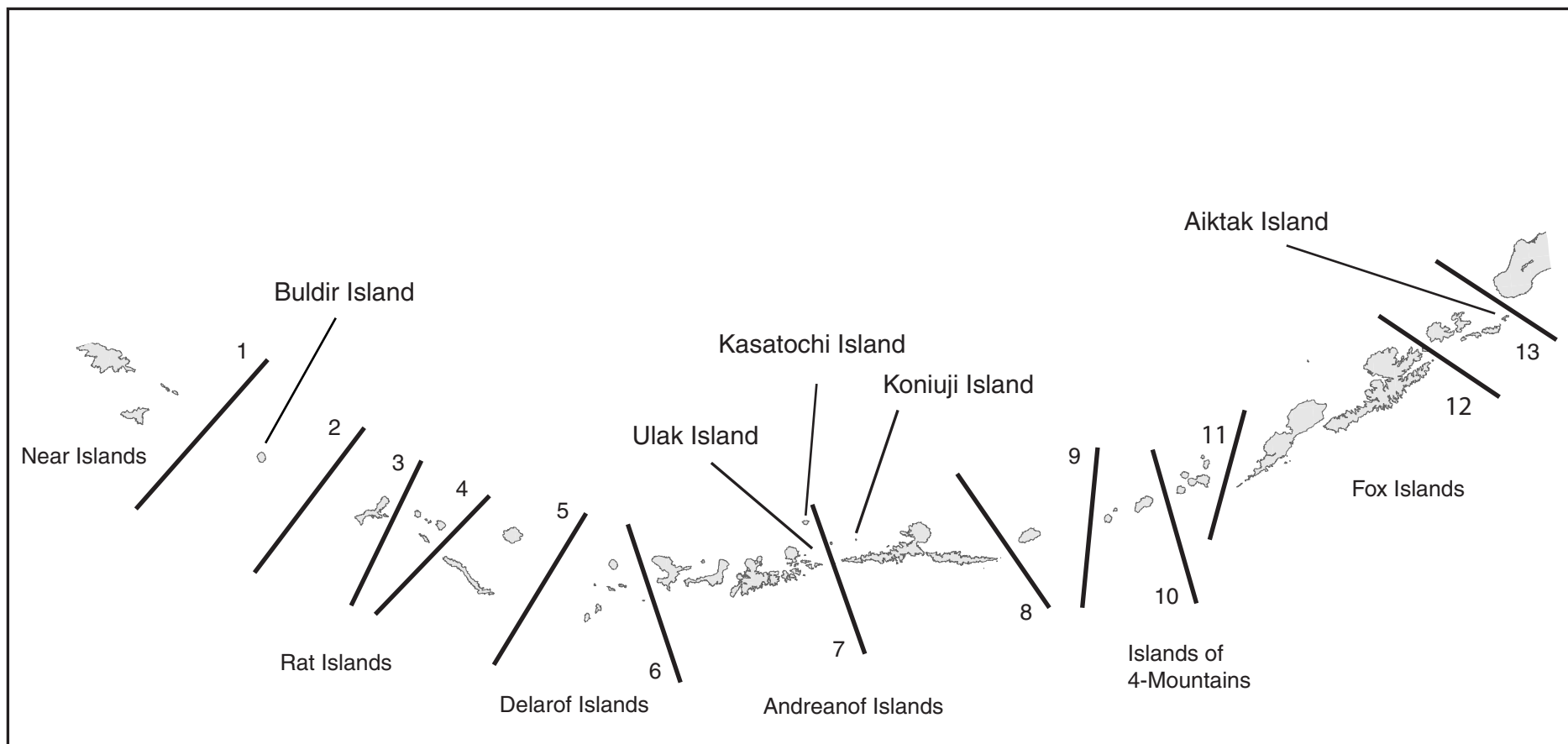
Figure captions:

Figure 1. Map of Aleutian Islands showing passes discussed in the paper, and annual seabird monitoring sites of the Alaska Maritime National Wildlife Refuge. Islands are separated into the eastern (between Unimak and Samalga pass), central (between Samalga and Amchitka Pass), and western Aleutians (from Amchitka Pass to the Near Islands).

Figure 2. Maps showing distribution of nesting colonies of (a) burrow and crevice nesting and (b) ledge and ground nesting seabirds in the Aleutian Islands. Data are from the Beringian Seabird Colony Catalog.

Figure 3. Population trends of (a) common and thick-billed murres, tufted puffins, black-legged and red-legged kittiwakes, and (b) Leach's and fork-tailed storm petrels, cormorants, glaucous-winged gulls and pigeon guillemots at Buldir, Kasatochi, and Aikta in the Aleutian Islands, 1972-2002. The Kasatochi monitoring sites includes two other islands (Ulak and Koniuji) because all species cannot be monitored at one site.

Figure 4. Box plots showing average rates of productivity (chicks per nest) for nine seabird species in the western (W), central (C), and eastern (E) Aleutians based on yearly estimates in the 1980s and 1990s.



Passes by number:

1. Buldir Pass
2. Kiska Pass
3. Segula Pass
4. Oglala Pass

5. Amchitka Pass
6. Tanaga Pass
7. Atka Pass
8. Seguam Pass

9. Amukta Pass
10. Yunaska Pass
11. Samalga Pass
12. Akutan Pass

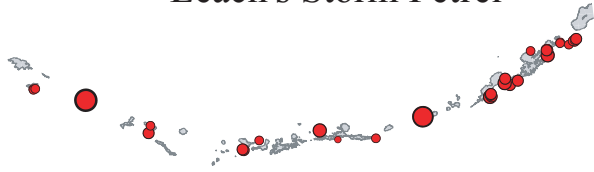
13. Unimak Pass



Burrow Nesters

Crevice Nesters

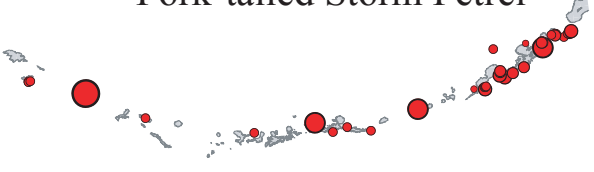
Leach's Storm Petrel



Least Auklet



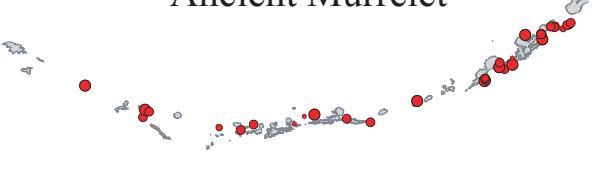
Fork-tailed Storm Petrel



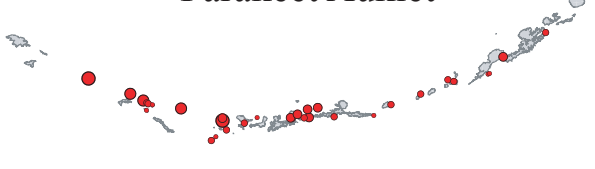
Crested Auklet



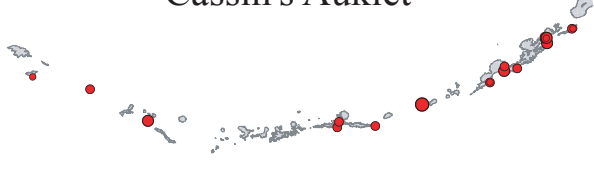
Ancient Murrelet



Parakeet Auklet



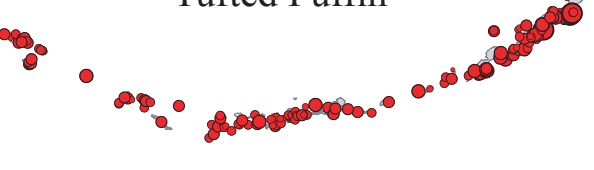
Cassin's Auklet



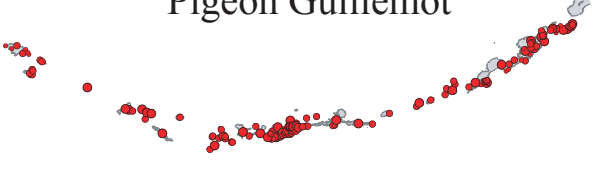
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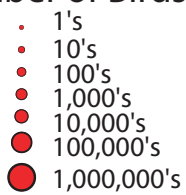
Tufted Puffin



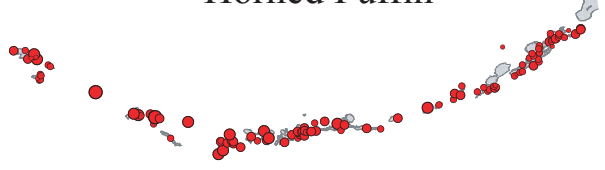
Pigeon Guillemot



Number of Birds

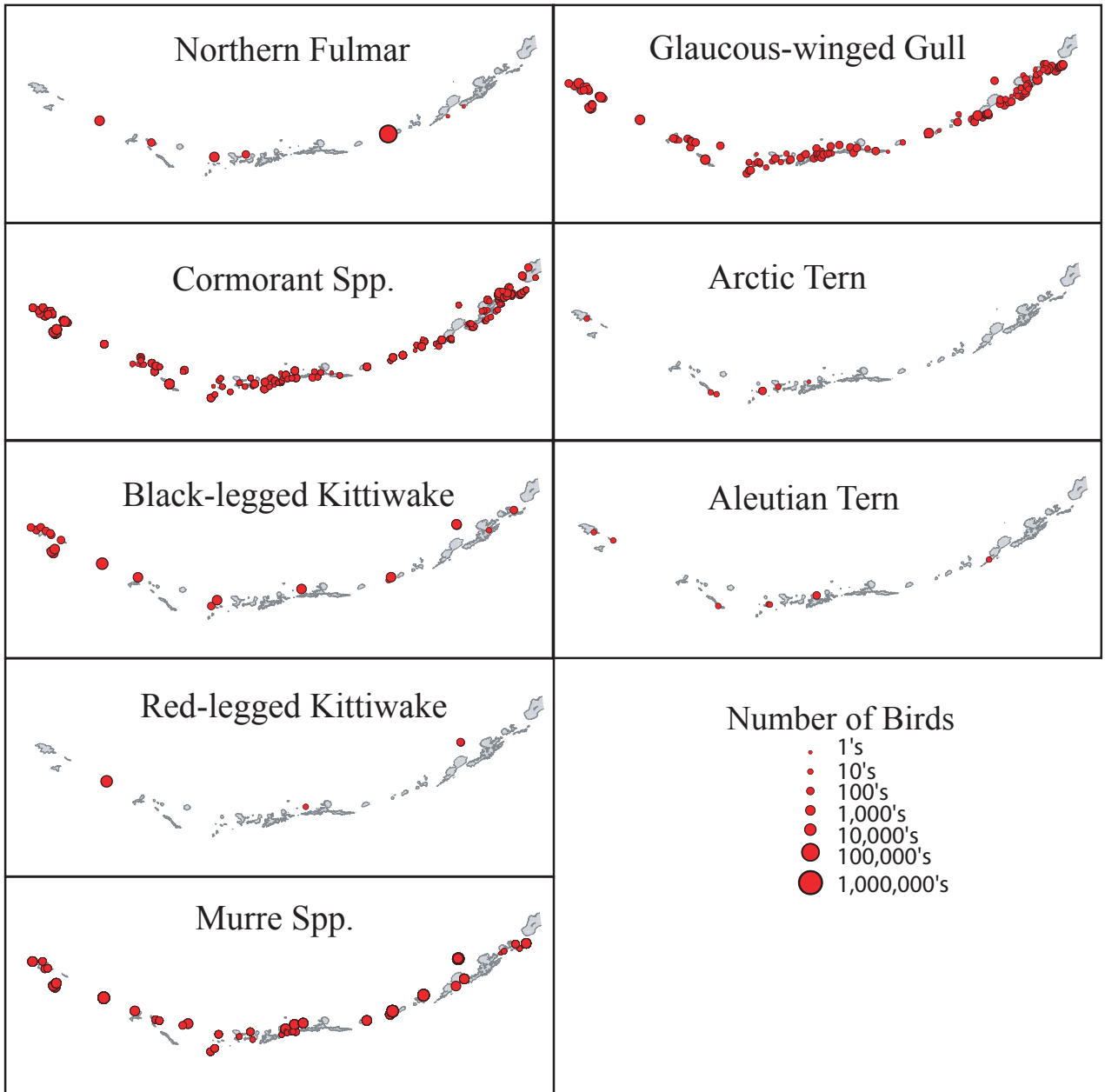


Horned Puffin

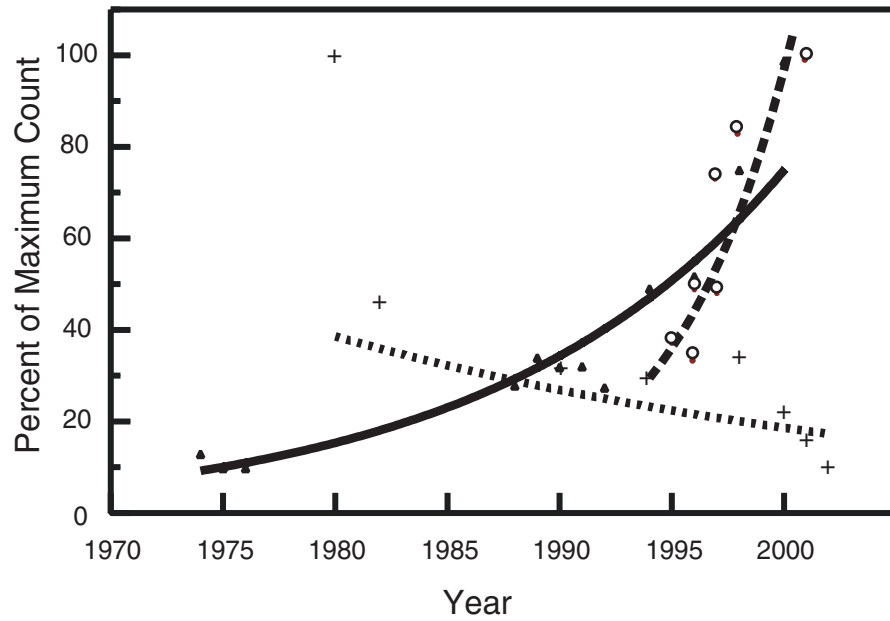


Ledge Nesters

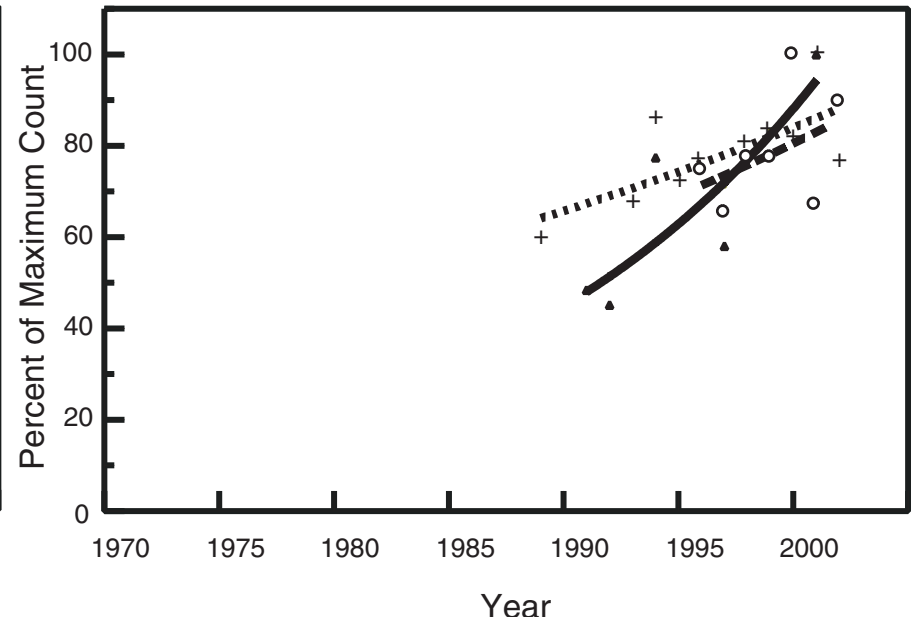
Ground Nesters



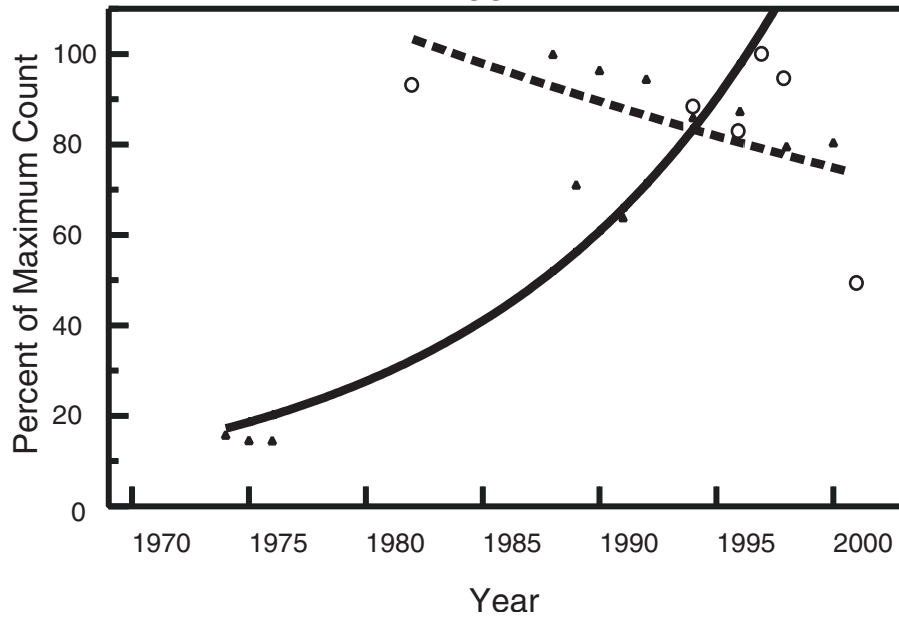
Common and Thick-billed Murres



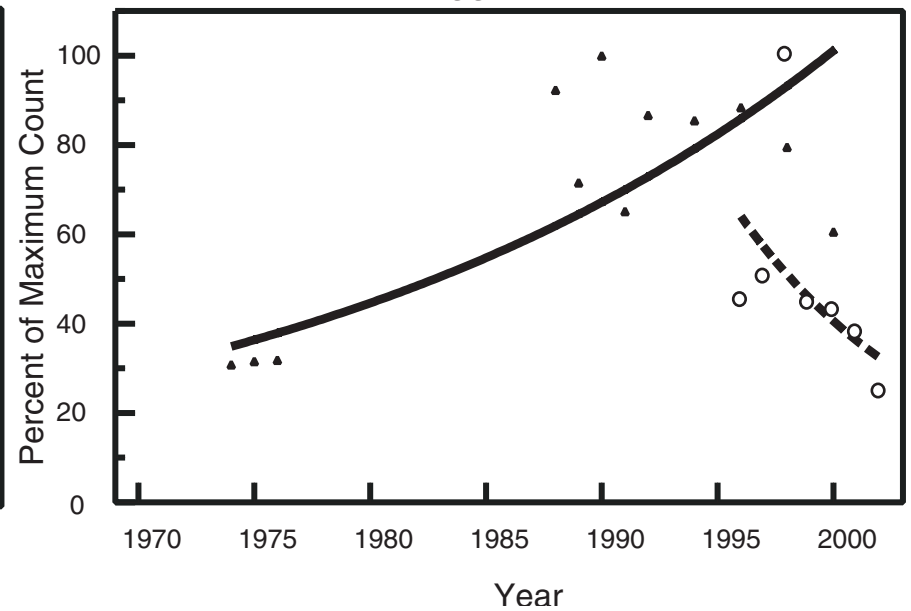
Tufted Puffin



Black-legged Kittiwake

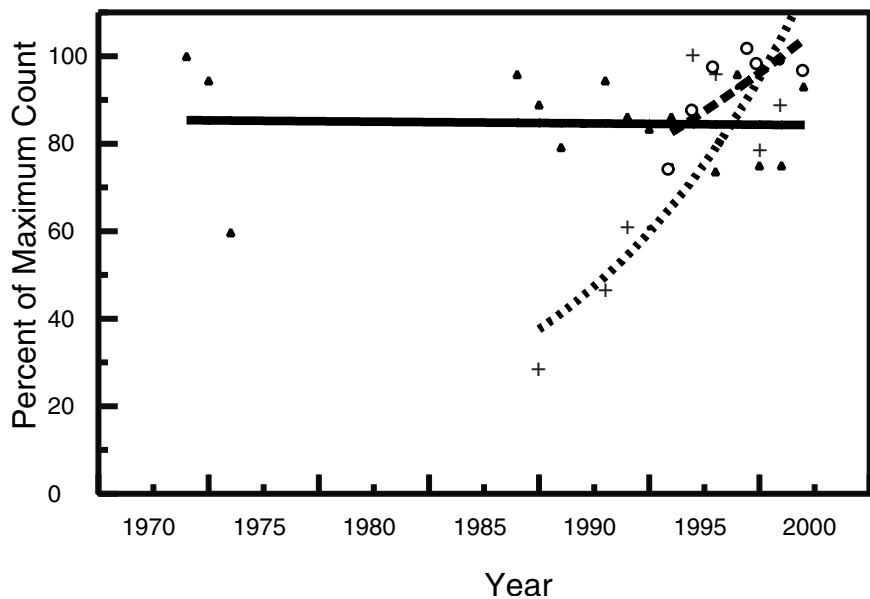


Red-legged Kittiwake

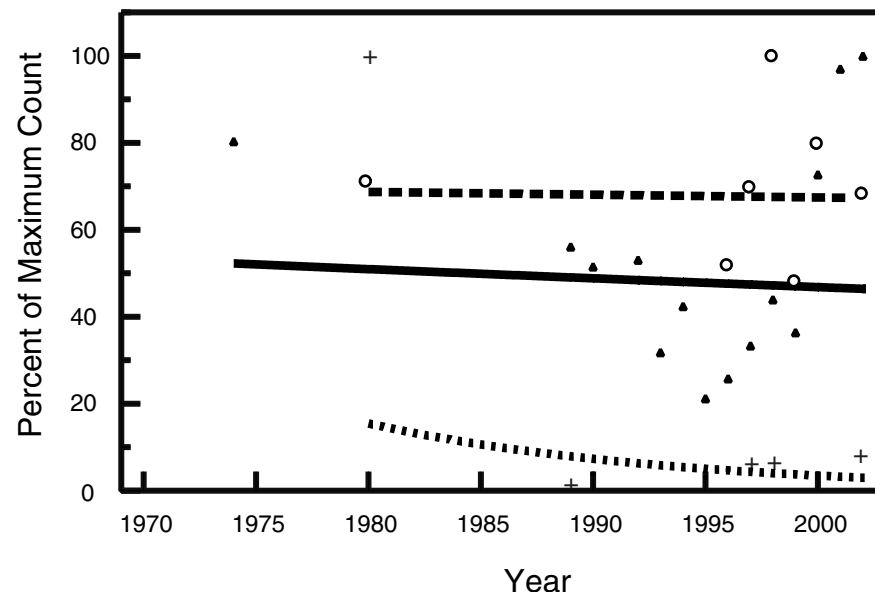


—▲ Buldir - - - - - ○ Kasatochi - - - - - + Aiktak

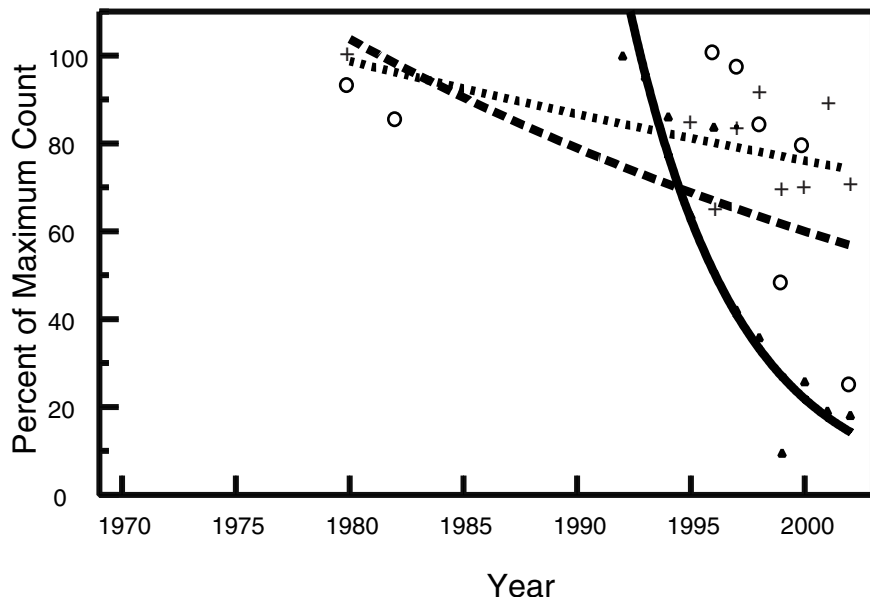
Leach's and Fork-tailed Storm Petrel



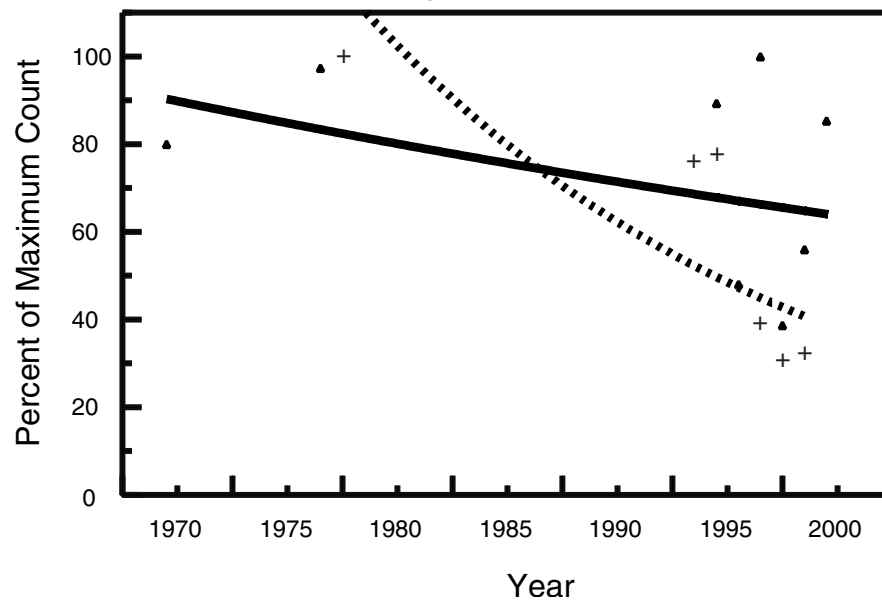
Cormorants



Glaucous-winged Gull



Pigeon Guillemot



Legend: —▲ Buldir - - - - - ○ Kasatochi - - - - - + Aiktak

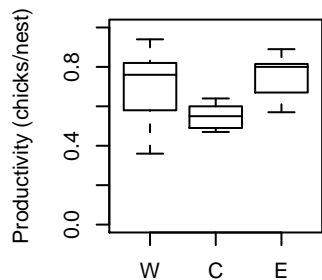
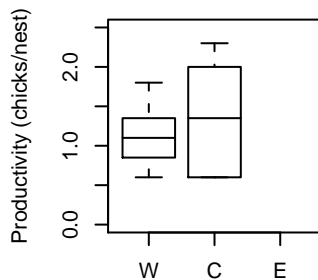
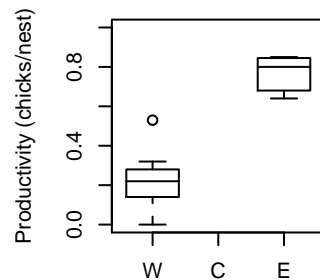
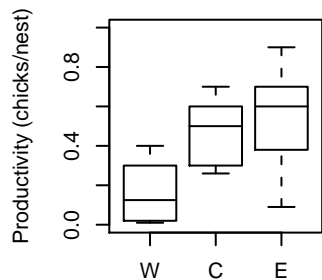
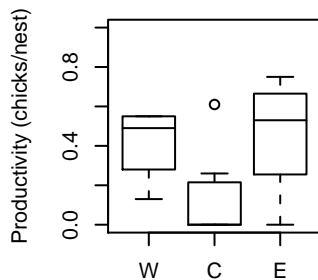
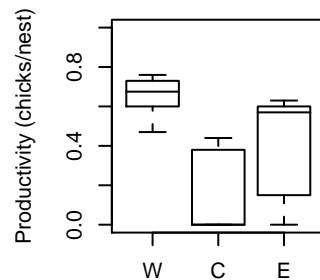
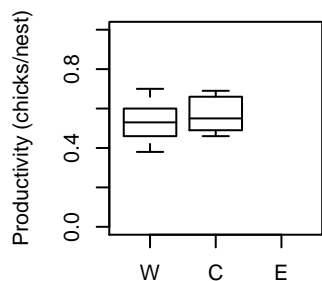
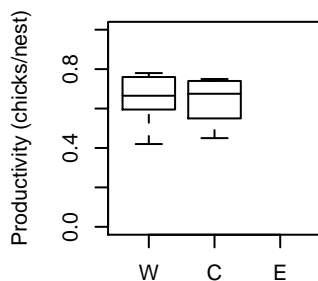
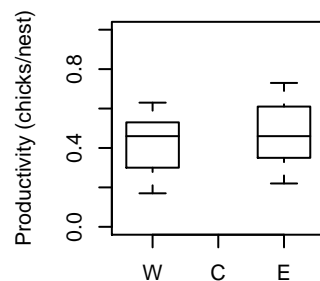
Fork-tailed Storm Petrel**Pelagic Cormorant****Glaucous-winged Gull****Black-legged Kittiwake****Common Murre****Thick-billed Murre****Least Auklet****Crested Auklet****Tufted Puffin**

Table 1. Feeding and nesting strategies of seabirds nesting in the Aleutian Islands.

<u>Species</u>	<u>Feeding Strategy</u>			<u>Nesting Strategy</u>
	Nearshore/offshore	Fish/Plankton	Dive/Surface	
Northern fulmar	Offshore	Fish	Surface	Surface
Storm-petrel spp.	Offshore	Plankton	Surface	Burrow
Cormorant spp.	Nearshore	Fish	Dive	Ledge
Glaucous-winged gull	Nearshore	Fish	Surface	Surface
Black-legged kittiwake	Offshore	Fish	Surface	Ledge
Red-legged kittiwake	Offshore	Fish	Surface	Ledge
Arctic tern	Nearshore	Fish	Surface	Surface
Aleutian tern	Nearshore	Fish	Surface	Surface
Murre spp.	Offshore	Fish	Dive	Ledge
Pigeon guillemot	Nearshore	Fish	Dive	Crevice
Brachyramphus murrelet	Nearshore	Fish	Dive	Surface
Ancient murrelet	Offshore	Plankton	Dive	Burrow
Cassin's auklet	Offshore	Plankton	Dive	Burrow
Parakeet auklet	Nearshore	Plankton	Dive	Crevice
Least auklet	Offshore	Plankton	Dive	Crevice
Whiskered auklet	Nearshore	Plankton	Dive	Crevice
Crested auklet	Offshore	Plankton	Dive	Crevice
Horned puffin	Nearshore	Fish	Dive	Crevice
Tufted puffin	Offshore	Fish	Dive	Burrow

Table 2. Factors affecting the colony sizes of Aleutian seabirds analyzed with a linear regression model of $\ln(n+1)$ transformed count data (birds). We consider $p < 0.1$ to be a significant result.

	Distance to large pass		Distance to medium or large pass		Island Area		Island Group
	Sign of Coeff	P	Sign of Coeff	P	Sign of Coeff	P	P
Northern fulmar	-	0.030	+	0.622	+	0.171	0.678
Storm-petrels	+	0.857	+	0.926	-	0.955	0.239
Cormorants	+	0.438	+	0.702	+	0.000	0.002
Glaucous-winged gull	+	0.585	-	0.702	+	0.001	0.001
Black-legged Kittiwake	-	0.054	+	0.061	+	0.306	0.025
Red-legged kittiwake	-	0.353	+	0.184	-	0.597	0.194
Arctic tern	-	0.092	+	0.130	+	0.051	0.228
Aleutian tern	-	0.067	+	0.042	+	0.001	0.076
Murres	-	0.962	+	0.764	+	0.193	0.628
Pigeon guillemot	+	0.001	-	0.832	+	0.000	0.066
Brachyramphus murrelets	-	0.699	+	0.016	+	0.005	0.121
Ancient murrelet	+	0.034	+	0.396	-	0.805	0.144
Cassin's auklet	+	0.975	+	0.07	+	0.955	0.622
Parakeet auklet	-	0.886	-	0.390	+	0.029	0.061
Least auklet	+	0.913	-	0.126	+	0.128	0.024
Whiskered auklet	+	0.130	-	0.234	+	0.037	0.361
Crested auklet	-	0.760	-	0.112	+	0.071	0.118
Horned puffin	+	0.28	+	0.487	+	0.000	0.000
Tufted puffin	+	0.004	+	0.054	+	0.273	0.014

Table 3. Predicted mean population size of seabird in each geographic area in the Aleutians, generated in a linear model holding distance to pass and island size constant. The p-values shown are for the multiple comparisons test of each group against the average of the other island groups (indicating whether that group differs in predicted colony size from the rest of the Aleutians). No values are presented for species for which the linear model indicated there were no significant differences ($p < 0.1$) among island groups.

	p for diff in groups	Western			Central			Eastern		
		observed	predicted	P	observed	predicted	P	observed	predicted	P
Northern fulmar	0.678									
Storm-petrels	0.239									
Cormorants	0.002	153	196.1	0.014	12	26.3	0.003	12.9	49.2	0.206
Glaucous-winged gull	0.001	466.6	309.7	0.009	37.7	32.4	0.004	66.4	69.7	0.249
Black-legged Kittiwake	0.025	8.2	2.7	0.014	0.8	0.6	0.430	0.7	1.5	0.430
Red-legged kittiwake	0.194									
Arctic tern	0.228									
Aleutian tern	0.076	1.2	0.8	0.054	0.2	0.5	0.569	0.1	0.7	0.569
Murres	0.628									
Pigeon guillemot	0.066	64.3	92.2	0.938	40.8	62.7	0.855	27.6	21.6	0.872
Brachyramphus murrelets	0.121									
Ancient murrelet	0.144									
Cassin's auklet	0.622									
Parakeet auklet	0.061	17.5	8	0.015	4	2.8	0.197	0.2	1	0.008
Least auklet	0.024	15.3	6.6	0.011	0.8	0.9	0.395	0	0.8	0.352
Whiskered auklet	0.361									
Crested auklet	0.118									
Horned puffin	0.000	398.9	416.1	0.000	66.8	84.6	0.001	2.8	4.7	0.000
Tufted puffin	0.014	1143.3	2727.6	0.164	147.6	191.4	0.041	643	82.8	0.254

Table 4. Summary of abundance of seabird species on 129 Aleutian Islands, Alaska. Data are best estimates from the Beringian Seabird Colony Catalog (USFWS 2000) with some more current data from recent AMNWR surveys. Species are ordered by total abundance.

Species	# Colonies	% of islands	Total # birds
Storm-petrel spp.	51	40	4802848
Least auklet	8	6	2278250
Tufted puffin	103	81	1214907
Crested auklet	10	8	873448
Northern fulmar	9	7	510520
Murre spp.	37	29	210249
Cassin's auklet	20	16	118640
Whiskered auklet	48	37	115839
Horned puffin	81	63	90404
Black-legged kittiwake	15	12	70073
Parakeet auklet	35	27	66227
Glaucous-winged gull	106	82	56714
Ancient murrelet	40	31	52756
Cormorant spp.	81	64	34897
Pigeon guillemot	109	85	14804
Red-legged kittiwake	4	2	4615
Brachyramphus murrelet	5	4	900
Aleutian tern	7	5	857
Arctic tern	6	5	845

Appendix A. Estimates of seabirds at breeding colonies in the Aleutian Islands from USFWS (2000) and more recent unpublished data from Alaska Maritime National Wildlife Refuge.

Island	ALTE ¹	ANMU	ARTE	BLKI	Brachy	CAAU	CORM	CRAU	GWGU	HOPU	LEAU	MURR	NOFU	PAAU	PIGU	RLKI	STPE	TUPU	WHAU
Attu	140	25	70	1682	500	0	4812	0	5818	9571	0	7691	50	300	110	0	0	16910	300
Agattu	0	15	0	7400	50	50	1641	0	3964	237	0	7714	0	120	168	0	2500	37018	200
Alaid	0	0	0	442	0	0	375	0	906	100	0	0	0	0	42	0	0	582	0
Nizki	15	0	15	0	0	0	637	0	1481	50	0	18	0	0	51	0	0	628	0
Shemya	0	0	0	0	0	0	542	0	1170	0	0	0	0	0	2	0	0	640	0
Buldir	0	10000	0	44280	0	400	480	280000	5000	20000	140000	13400	1240	12000	300	4400	3000000	20000	30000
Kiska	0	0	0	839	0	0	290	332000	900	5500	1160000	0	0	4000	560	0	0	10000	0
Little Kiska	0	175	0	0	0	0	28	0	400	3000	0	0	0	0	350	0	0	6600	0
Tanadak (W)	0	0	0	0	0	0	18	0	60	50	0	0	0	0	24	0	0	30	0
Segula	0	0	0	0	0	0	140	46975	210	550	474150	0	0	1620	144	0	0	550	0
Khvostof	0	0	0	0	0	0	24	0	230	4500	0	0	0	30	60	0	0	1290	0
Pyramid	0	0	0	0	0	0	5	0	75	700	0	0	0	0	22	0	0	900	0
Tomfredof	0	2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1500	0	50
Davidof	0	0	0	0	0	0	260	0	350	11600	0	620	120	28	160	0	0	7060	0
Rat	0	125	0	0	0	3500	170	0	384	56	0	0	0	2	56	0	2000	210	0
Little Sitkin	0	115	0	0	0	0	36	0	284	660	0	246	0	4	218	0	0	400	106
Amchitka	500	0	500	0	0	0	4000	0	2000	100	0	0	0	0	150	0	50	1400	0
Semisopochnoi	0	0	0	0	0	0	212	5000	1000	4500	85000	3568	0	1700	40	0	0	3500	0
Amatignak	0	0	0	0	0	0	132	0	200	1400	0	236	0	32	70	0	0	450	0
Tanadak (E)	0	0	0	0	0	0	0	0	120	0	0	0	0	0	0	0	0	0	0
Ulak (W)	0	0	0	0	0	0	12	0	200	2500	0	182	0	8	210	0	0	2700	0
Dinkum Rocks	0	0	0	0	0	0	0	0	12	250	0	0	0	0	14	0	0	0	0
Unalga	0	0	0	654	0	0	10	0	50	80	0	0	0	0	90	0	0	750	0
Kavalga	0	0	0	0	0	0	0	0	90	520	0	0	0	0	80	0	0	1200	0
Ogliuga	12	0	80	0	0	0	13	48	140	750	0	0	0	10	190	0	0	50	0
Egg	0	0	0	0	0	0	0	0	12	20	0	0	0	0	14	0	0	20	0
Tag	0	0	0	0	0	0	0	0	16	300	0	0	0	40	40	0	0	800	0
Twin	0	0	0	0	0	0	0	0	34	0	0	0	0	0	2	0	0	0	0
Ugidak	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	20	0
Skagul	20	0	120	0	0	0	0	0	100	110	0	0	0	0	40	0	0	0	0
Gareloi	0	200	0	1890	0	0	3150	186000	240	3100	402000	360	5920	43200	36	0	5000	6500	200
Gramp	0	0	0	0	0	0	0	0	6	20	0	0	0	0	30	0	0	60	0
Ilak	0	0	0	0	0	0	20	0	30	900	0	0	0	0	90	0	0	550	0
Tidgituk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2000	200	0
Whip	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	1500	200	0

Island	ALTE	ANMU	ARTE	BLKI	Brachy	CAAU	CORM	CRAU	GWGU	HOPU	LEAU	MURR	NOFU	PAAU	PIGU	RLKI	STPE	TUPU	WHAU
Tanaga	0	118	0	0	0	0	72	125	584	640	0	20	0	25	200	0	0	1176	0
Castle	0	0	0	0	0	0	20	0	40	150	0	0	0	0	20	0	0	130	0
Kanaga	0	0	0	0	0	0	156	0	500	5300	0	96	0	0	450	0	0	16800	0
Bobrof	0	200	0	0	0	0	268	0	50	1300	0	1032	180	20	0	0	1200	600	0
Adak	150	0	60	0	0	0	1301	0	583	700	0	0	0	0	1233	0	0	768	0
Crone	0	0	0	0	0	0	0	0	0	106	0	0	0	0	179	0	0	1065	0
Kagalaska	0	0	0	0	0	0	158	0	0	111	0	0	0	0	525	0	0	68	0
Silak	0	0	0	0	0	0	6	0	0	0	0	0	0	0	2	0	0	0	0
Little Tanaga	0	0	0	0	0	0	118	0	136	98	0	0	0	0	449	0	0	0	0
Umak	0	0	0	0	0	0	22	0	214	280	0	52	0	0	234	0	0	190	0
Great Sitkin	0	0	0	0	0	0	8	0	543	0	0	0	0	0	340	0	0	0	0
Aziak	0	0	0	0	0	0	0	0	26	290	0	0	0	172	110	0	0	636	0
Asuksak	0	0	0	0	0	0	0	0	68	236	0	0	0	40	50	0	0	180	0
Tanaklak	0	0	0	0	0	0	0	0	20	0	0	0	0	0	146	0	0	0	0
Kanu	0	0	0	0	0	0	0	0	16	70	0	0	0	0	180	0	0	26	0
Tanadak & Box	0	0	0	0	0	0	18	0	80	100	0	0	0	0	176	0	0	196	0
Anagaksik	0	0	0	0	0	0	0	0	124	154	0	0	0	0	14	0	0	241	0
Igitkin	0	1	0	0	0	0	0	0	47	141	0	3	0	0	212	0	50	61	0
Ulak (E)	0	0	0	0	0	0	254	0	64	469	0	1195	0	125	20	0	0	91	8000
Chugul	0	0	0	0	0	0	26	0	119	99	0	49	0	0	230	0	0	146	0
Tagalak	0	0	0	0	0	0	0	0	10	12	0	0	0	0	8	0	0	9	0
Fenimore Islets	0	0	0	0	0	0	59	0	221	247	0	11	0	25	45	0	0	1248	0
Fenimore Rock	0	0	0	0	0	0	0	0	26	0	0	17	0	0	0	0	0	55	500
Ikiginak	0	0	0	0	0	0	30	0	11	50	0	53	0	2	42	0	0	430	500
Oglodak	0	0	0	0	0	0	104	0	47	315	0	111	0	109	39	0	0	735	500
Kasatochi	0	1	0	0	0	0	38	20000	107	11	15000	1000	0	1000	16	0	0	18	500
Atka	0	0	0	0	300	800	590	0	190	120	0	0	0	200	400	0	0	5600	0
Koniuji	0	10000	0	2330	0	0	22	300	300	200	2000	2293	0	300	62	15	250000	20000	20000
Salt	0	500	0	0	0	500	0	0	400	1200	0	0	0	0	0	0	0	3000	0
Sagchudak	0	500	0	0	0	0	30	0	350	100	0	0	0	20	90	0	500	200	0
Amtegis	0	0	0	0	0	200	0	0	0	0	0	0	0	0	10	0	300	1200	500
Amlia	0	0	0	0	0	0	76	0	280	900	0	0	0	0	980	0	0	7100	200
Round	0	1000	0	0	0	0	6	0	60	0	0	0	0	0	0	0	400	6000	100
Tanadak	0	200	0	0	0	500	0	0	10	50	0	0	0	10	50	0	600	1000	100
Seguam	0	0	0	0	0	0	160	0	20	200	0	2350	0	90	100	0	500	1160	30000
Amukta	0	0	0	28	0	50	90	0	4	0	0	1805	3000	200	72	0	500	0	2000
Chagulak	0	5000	0	6000	0	100000	116	3000	3000	3000	100	24700	500000	100	170	0	1000000	50000	200
Yunaska	0	0	0	0	0	0	210	0	6	40	0	0	0	0	30	0	500	60	2500

Island	ALTE	ANMU	ARTE	BLKI	Brachy	CAAU	CORM	CRAU	GWGU	HOPU	LEAU	MURR	NOFU	PAAU	PIGU	RLKI	STPE	TUPU	WHAU
Herbert	0	0	0	0	0	0	56	0	0	130	0	0	0	0	100	0	0	120	2000
Carlisle	0	0	0	0	0	0	44	0	0	200	0	0	0	50	80	0	500	800	2000
Chuginadak	0	0	0	0	0	0	580	0	120	460	0	0	0	40	130	0	5000	1040	2000
Uliaga	0	0	0	0	0	0	10	0	20	30	0	0	0	0	20	0	500	10	2000
Kagamil	0	0	0	0	0	0	150	0	0	0	0	34000	0	0	52	0	500	0	2000
Adugak	0	0	0	0	0	0	20	0	347	0	0	0	0	0	62	0	50	0	4
Umnak	20	0	0	0	0	0	20	0	347	0	0	0	0	0	62	0	0	0	4
Ananiuliak	0	0	0	0	0	0	122	0	1500	0	0	0	0	0	246	0	100	0	2
Kigul Islet 8	0	0	0	0	0	0	28	0	400	8	0	0	0	0	20	0	0	0	0
Kigul Islet 3	0	0	0	0	0	0	0	0	500	12	0	0	0	0	14	0	0	0	0
Kigul Islet 2	0	0	0	0	0	0	40	0	240	0	0	0	0	0	8	0	2000	3600	0
Kigul Islet 4	0	0	0	0	0	0	70	0	0	8	0	0	0	0	16	0	0	0	0
Kigul Islet 5	0	0	0	0	0	0	50	0	90	0	0	0	0	0	0	0	0	100	0
Kigul Islet 6	0	200	0	0	0	150	0	0	0	0	0	0	0	0	0	0	5000	16514	0
Kigul Islet 7	0	75	0	0	0	0	0	0	280	0	0	0	0	0	6	0	1500	5690	6
Pancake Rocks	0	0	0	0	0	0	24	0	185	0	0	0	0	0	0	0	0	0	0
Vsevidof	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ogchul	0	1000	0	0	0	0	0	0	400	0	0	0	4	10	94	0	1200	57970	0
Kigul	0	300	0	0	0	100	0	0	900	0	0	0	0	0	80	0	7000	800	6
The Pillars	0	0	0	0	0	0	0	0	0	0	0	4000	0	0	0	0	0	0	0
Fire Island	0	0	0	2300	0	0	40	0	0	10	0	39300	0	0	0	0	0	300	0
Bogoslof	0	0	0	1822	0	0	250	0	1698	0	0	41415	0	0	0	200	500	5000	0
Unalaska	0	2706	0	28	0	1000	1114	0	3329	261	0	0	6	0	203	0	31000	67553	10
Hog	0	0	0	0	0	0	0	0	200	54	0	0	0	0	142	0	0	0	0
Tanaskan Bay Islands	0	0	0	0	0	0	0	0	180	0	0	0	0	0	198	0	0	3106	0
Dushkot	0	0	0	32	0	0	0	0	0	0	0	0	0	0	96	0	0	3645	0
Ogangen	0	0	0	0	0	0	34	0	904	126	0	0	0	0	82	0	2000	34450	0
Peter	0	0	0	0	0	0	60	0	66	0	0	0	0	0	24	0	0	2879	0
Greg	0	0	0	0	0	0	0	0	20	44	0	0	0	0	180	0	0	0	0
Wilsow	0	3000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	240	10000	20
Emerald	0	3000	0	0	0	3000	0	0	314	0	0	0	0	0	0	0	124382	31863	6
Ship Rock	0	0	0	0	0	0	0	0	60	0	0	6500	0	595	80	0	3300	66	0
Pustoi	0	550	0	0	0	400	0	0	404	0	0	0	0	0	110	0	13500	14140	0
Auklet (Baby)	0	200	0	0	0	3500	0	0	0	0	0	0	0	0	30	0	500	41696	750
Tangam (Baby)	0	600	0	0	0	0	0	0	0	0	0	0	0	0	150	0	3000	27331	750
Excelsior (Baby)	0	400	0	0	0	2000	98	0	30	0	0	12	0	0	115	0	4500	40201	750
Adokt (Baby)	0	700	0	0	0	40	142	0	60	40	0	0	0	0	70	0	2000	25492	750
Koschekt (Baby)	0	300	0	0	0	0	0	0	130	0	0	0	0	0	34	0	5000	10998	750

Island	ALTE	ANMU	ARTE	BLKI	Brachy	CAAU	CORM	CRAU	GWGU	HOPU	LEAU	MURR	NOFU	PAAU	PIGU	RLKI	STPE	TUPU	WHAU
Rootok	0	0	0	0	0	0	88	0	20	74	0	0	0	0	8	0	0	0	0
Akutan	0	0	0	0	0	0	4346	0	114	323	0	22	0	0	112	0	0	3540	100
Akun	0	400	0	0	0	0	738	0	495	8	0	0	0	0	166	0	200	54214	100
Puffin	0	200	0	0	0	0	0	0	0	0	0	0	0	0	45	0	900	35374	100
Poa	0	1000	0	0	0	0	0	0	1060	0	0	0	0	0	15	0	5700	33484	25
Tangik	0	350	0	0	0	0	38	0	350	0	0	0	0	0	18	0	4800	20228	10
Tanginak	0	0	0	346	0	0	708	0	182	4	0	1100	0	0	12	0	0	0	0
Derbin	0	100	0	0	0	0	108	0	1318	6	0	23	0	0	34	0	1400	9485	4
Tigalda	0	0	0	0	0	0	164	0	100	304	0	0	0	0	270	0	0	390	0
Kaligagan Islets	0	500	0	0	0	400	36	0	355	0	0	55	0	0	264	0	976	21634	18
Kaligagan	0	1000	0	0	0	50	280	0	2000	0	0	0	0	0	328	0	13000	111082	18
Aiktak	0	1000	0	0	0	0	1734	0	2750	32	0	15000	0	0	68	0	23500	102428	0
Ugamak	0	0	0	0	0	0	0	0	126	268	0	0	0	0	142	0	0	1392	0

¹Species codes are: ALTE – Aleutian tern, ANMU – Ancient murrelet, ARTE – Arctic tern, BLKI – Black-legged kittiwake, Brachy – Brachyramphus murrelet, CAAU – Cassin’s auklet, CORM – Cormorant spp., CRAU – Crested auklet, GWGU – Glaucous-winged gull, HOPU – Horned puffin, LEAU – Least auklet, MURR – Murre spp., NOFU – Northern fulmar, PAAU – Parakeet auklet, PIGU – Pigeon guillemot, RLKI – Red-legged kittiwake, STPE – Storm-petrel spp., TUPU – Tufted puffin, WHAU – Whiskered auklet